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A DESCRIPTION OF A SUBHUMID CORRIDOR ACROSS NORTHERN CENTRAL AMERICA, WITH COMMENTS ON ITS HERPETOFAUNAL INDICATORS

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INTRODUCTION

IT IS well known that deserts, or at least subhumid climatic conditions, along the east coasts of land masses within the limits of the tropics are extremely rare. Theoretically, in fact, subhumid climates cannot possibly occur in such locales. Yet where rain-shadow conditions exist or where local air movements produce abnormal conditions, dry-lands do occur in certain tropic east-coast areas. Two such regions in northern Central America have long been known to biologists, the Comayagua Valley of Honduras and the valley of the middle and upper Río Motagua in Guatemala (see Map 1 for the locations hereinafter mentioned).

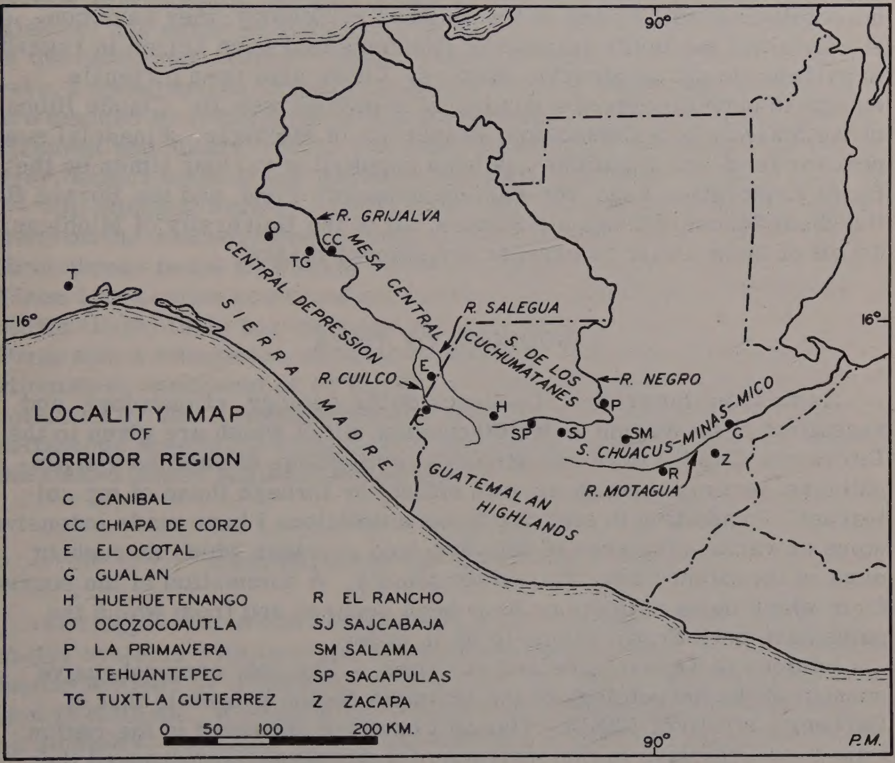
For some years I have been accumulating data on the fauna of the latter region as well as on that of the adjacent dry-lands of central Guatemala, and, as a result, some rather interesting geographic anomalies have been uncovered. As yet no faunal data on the Comayagua Valley have been forthcoming.

Of particular interest is the fact that certain groups of reptiles and amphibians are rather extensively distributed over the drier parts of central and southeastern Guatemala and along the none-too-mesic Pacific versant of eastern Guatemala and El Salvador and in some cases as far south as Costa Rica. The immediate systematic affinities of these groups are found in southern Mexico despite the fact that there is no geographic continuity in the Mexican and Central American populations along the lowlands of either the Pacific or Caribbean,where continuity would normally be sought. In order to explain this perplexing situation I was led to examine the distribution and the faunas of the various dry-land environments of northern Central America and southern Mexico.

As a result of investigations carried on particularly in 1952 and 1953, it was discovered that a chain of dry-land environments extends from the Isthmus of Tehuantepec (Pl. I, Fig. 1) to the xeric Motagua Valley of Guatemala, from which there are ample subhumid pathways (Pl. I, Fig. 2) for dispersal both eastward into Honduras and southward to lower Central America. The crux to the solution of the whole problem, however, is the corridor that connects the Isthmus of Tehuantepec with the middle Motagua Valley. It is the purpose of this paper to call to the attention of biologists this dry-land corridor that crosses northern Central America. As yet information is very incomplete, and the evidence herein presented is at best scanty, but it is hoped that a presentation of my own findings at this time may prove of some service to investigators working with the distributions of groups other than the amphibians and reptiles.

This corridor cuts through the highlands of Chiapas and Guatemala and, with the exception of narrow breaks, lies for the most part below elevations of 1000 m. The environment throughout the length of the corridor is essentially subhumid and, though broken at higher elevations by oak and pine forests, supports a cover of dry-forest, grassland, and desert vegetation types. Though various biologists have at several times recognized the distinctness of the environment at either end of the corridor, none has ever given consideration to the possibility of its continuity across the Central American isthmus. Smith (1939) placed the Grijalva (Mexican) section in his Chiapan Plateau Biotic Province. Goldman and Moore (1945) considered this section to be a part of their Tehuantepec Biotic Province, which included in addition to the Grijalva Valley and the Isthmus of Tehuantepec dry-lands the Pacific coastal plain of Chiapas and Guatemala. Goldman (1951) did not modify this scheme. Smith (1949) included the Mexican section in his Palenque Province,which he considered as a part of the Atlantic Subregion,and thus inferred closer relationship to the mesic Caribbean versant than to the drier Pacific side. At the other end of the corridor in Guatemala Stuart (1943) recognized the distinctness of the dry-lands of Guatemala in referring them to his Zacapan Biotic Province, and Smith (1949) followed this same scheme. Neither of these two works, however, recognized any relationship between the Mexican and Guatemalan sections. This paper will not give consideration to the faunal position of the different parts of the corridor, but will be limited to a description and a discussion of the biological significance of the region.

Though I had visited such parts of the corridor as the Salamá Basin (Schmidt and Stuart, 1941) and the lower Río Negro and Motagua sections as early as 1938, it was not until 1947 that I became concerned with the Mexican section as a result of a visit to the Cuilco Valley in the headwaters of the Río Grijalva. Finally, in 1952 and 1953 I was able to visit and study the entire Mexican part of the corridor from Tehuantepec through the Central Depression of Chiapas, and in the former year I was also able to investigate in some detail the Motagua division. It was these last investigations that crystallized the ideas which are presented herein.



Map 1

The maps of the distributions of the several species of lizards have been compiled from a number of sources. I have included, therefore, only the localities of which I am reasonably certain, and the majority of those through the corridor have been checked personally. In the case of *Enyaliosaurus*, *clarki* occurring in Guerrero could not be shown. In other instances only pertinent records are shown in extralimital regions.

Acknowledgments

In gathering data for this paper I have had the close co-operation of many individuals and institutions. For the privilege of examining collections in their charge (some of them unstudied) I am indebted to Mr. Charles E. Bogert of the American Museum of Natural History, Mr. Clifford Pope of the Chicago Natural History Museum, Dr. Edward H. Taylor of the University of Kansas, and Dr. Doris Cochran of the United States National Museum. I am particularly indebted to my colleagues at the University of Michigan, Dr. Norman E. Hartweg and Dr. Charles M. Walker. In addition to permitting me access to the herpetological collections of the Museum of Zoology, they have constantly aided me in the solution of problems that have arisen in regard to systematic and geographic matters. I have also been fortunate enough to have discussed a number of problems with Dr. Claude Hibbard of the Museum of Paleontology, University of Michigan. Financial support for field investigations has been supplied at various times by the Baird Exploration Fund, the Faculty Research Fund, and the Horace H. Rackham School of Graduate Studies, all of the University of Michigan. To all of these I wish to express my sincere thanks.

SOURCES OF DATA

Aside from the technical sources on the geology, climatology, and vegetation of the region under discussion, all of which are given in the Literature Cited, I have had access to collections of reptiles and amphibians secured through my own efforts or through those of my colleagues. In addition to studying these collections I have made extensive notes on various features of this dry-land corridor which throughout most of its extent I have visited personally. A summation of the sources from which these collections have been secured and from which the notes have been drawn seems to be in order.

Isthmus of Tehuantepec and environs. — The only comprehensive account of the herpetology of the isthmian region proper is that of Hartweg and Oliver (1940). Though I have not collected in the region, I spent several days in the environs of Tehuantepec and crossed the Isthmus to the wet forest on the Gulf of Mexico side. I have also crossed the Inter-American Highway which traverses the entire length of the Tehuantepec plains before climbing over the Sierra Madre into the Grijalva Valley. This last trip I have made on four different occasions.

Middle Grijalva Valley. — Smith (1946) has supplied some knowledge of the herpetofauna in the region of Ocozocoautla. I have also had access to material collected by my colleague, Norman E. Hartweg, who spent some days in the vicinity of Chiapa de Corzo. I have passed through the region on several occasions.

Upper Grijalva Valley. — I have studied this region briefly in both Mexico and Guatemala. In 1947, while studying the southwestern highlands of Guatemala, I crossed the Sierra Madre and descended into the valley of the Río Cuilco at Canibal close to the Mexican border, where I spent several days collecting. In 1953 I spent four days collecting in the region of El Ocotal (Ciudad Cuauhtémoc) near the Guatemalan border. Here most of my collecting was done along the Río San Gregório and on the flats drained by small tributaries of that river which joins with the Cuilco and lesser streams to form the Grijalva.

Río Negro Valley. — Although I have spent several days in Sacapulas, I have never done any extensive collecting in the region. From farther downstream, north of Cubulco, the British Museum (Natural History) has some material which was collected during the latter half of the nineteenth century. Below that point at Chixoy, near La Primavera, I spent several days collecting in 1940. Of the higher basins that are drained by tributaries of the Río Negro only that of Salamá is known (Schmidt and Stuart, 1941). I passed through all of these basins, however, when I made a foot journey from Salamá to Sacapulas in 1944.

Río Motagua Valley. — During the course of carrying on investigations on the southeastern uplands of Guatemala in 1952, I spent some three weeks in the El Rancho region, both at the village itself and at Finca Los Leones in a tributary valley to the northwest of El Rancho. Slevin (1939, 1942) has reported on material which he collected at Progreso, a village in a tributary valley of the Motagua, only a few kilometers southwest of El Rancho. I have also had access to material collected by Mr. Townsend Sackett in the Zacapa region. A few miscellaneous specimens from Gualán are preserved in the collections of the United States National Museum.

DESCRIPTION OF THE CORRIDOR

Geology. — Inasmuch as the corridor is made up of three separate valley systems with intervening mountain ranges and in places small basins drained by tributaries of the main streams, a geological summation is difficult. It is necessary, therefore, to treat each major valley as an entity. Needless to say, the summary works of Schuchert (1935) and Sapper (1937) are the authorities on which the following description is based.

The corridor begins in the north with the valley of the Río Grijalva. This valley, more generally known as the Central Depression of Chiapas, is oriented roughly in a northwest-southeast direction. To the southwest it is bounded by the Sierra Madre which, beginning as a low range at the Isthmus of Tehuantepec (long. 94°), increases in height toward the southeast and terminates in southwestern Guatemala (long. 92°). On the northeast side of the depression the Mesa Central rises in a sharp escarpment. Though several geologically distinct blocks are involved, this Mesa Central presents an upland area that is more or less continuous with the Sierra de los Cuchumatanes of southwestern Guatemala. Between these two highland masses the Central Depression lies as a graben whose northwestern entrance opens into the Isthmus of Tehuantepec and whose southeastern end abuts the Sierra de los Cuchumatanes. The valley has a length of about 175 km. and a maximum width of possibly 50 km.

Cretaceous limestones outcrop more or less continuously throughout the length of the valley, and these beds are apparently of the same formations that occur in southwestern and central Guatemala. Though the Sierra Madre is composed of ancient sedimentary and igneous rocks, some of which are apparently of Permian age, the Mesa Central is composed entirely of young sedimentaries, some as recent as Miocene. The graben-horst structure of the Central Depression and its bordering highlands was unquestionably the result of the Pliocene orogeny which was responsible for most of the extant configuration of northern Central America.

Throughout its course in the graben the fall of the Río Grijalva is slight. Its flood plain in the neighborhood of the Guatemalan border lies at an elevation of about 700 m., and at the lower end of the valley at Chiapa de Corzo it has an elevation of about 400 m. The floor of the depression, however, is by no means level. Tributaries of the Grijalva, especially from the south, have dissected the valley slopes and floor to produce terrain of moderate to high relief in various places. At no locality within the graben are elevations in excess of 1200 m. encountered.

At the upper (Guatemalan) end of the valley the Río Grijalva takes on a frayed appearance as its tributaries from the Sierra de los Cuchumatanes and from the Sierra Madre converge to form the main stream. The graben structure of the valley, too, comes to an end, and canyon-like tributary valleys slash back into the mountains. Some of these valleys appear to follow structural lines, whereas others appear to be entirely erosional in their origins. My interest lies in only two of these valleys, that of the Río Saleguá, whose lower course in Mexico is known as the San Gregório, and that of the Río Cuilco.

Throughout its course in Guatemala the Saleguá flows through a narrow V-shaped valley that lies between the southern edge of the Sierra de los Cuchumatanes and a local highland block known as the Sierra de Cuilco. The valley, which is a linear projection of the Central Depression of Chiapas, is probably structural. The gradient of the stream through this part of its course is considerable, its fall amounting to no less than 1000 m. between its source in the Huehuetenango region and the Mexican border, a distance of about 65 air-line kilometers.

The Cuilco through most of its course similarly occupies a deep V-shaped valley (Pl. III, Fig. 1). Arising on the crest of the Sierra Madre in Guatemala, the stream flows eastward, loops around the eastern and northern sides of the Sierra Madre, and continues northwestward to join the San Gregório in the eastern end of the Central Depression. The gradient of the Cuilco, like that of the Saleguá, is considerable, and at least part of its course, where it passes between the Sierra Madre and the Sierra de Cuilco, is canyon-like. At the eastern end of the Sierra de Cuilco, the Saleguá and Cuilco are separated by only a narrow, low ridge. The valley of the Cuilco is probably erosional rather than structural.

The Grijalva drainage comes to an end on the rolling uplands in the vicinity of Huehuetenango, where the continental divide attains an elevation of roughly 1900 m. (Pl. IV, Fig. 1). To the east of the divide are encountered the headwaters of the Río Negro. Though the source of this stream is generally taken as a large spring in the vicinity of Aguacatán, most of the waters of the upper river are derived from the plateau lands to the south.

Intrenched in a narrow valley from its very source, the Negro plunges into a gorge at the level of Sacapulas and continues to flow in a deep canyon due eastward for a matter of some 60 km. In a great S-shaped flexure it then breaches the highlands of El Quiché and Alta Verapaz (Pl. IV, Fig. 2) and flows out onto the lowlands of the Yucatán Peninsula toward the north. The origin of this upper valley of the Río Negro is obscure, and it is evident that the history of drainage lines through this region has been extremely complex. Nevertheless, it seems fairly certain that the extant gorge of the Negro is structural and dates from the Pliocene. It lies just to the south of a great fault that separates the younger limestone mountains (the Cuchumatanes and the Sierra de Uspantán) on the north from the ancient and extremely complex mass (Sierra de Chuacús) to the south. Like the headwaters of the Grijalva, the Negro in its upper course has a steep gradient, falling between its source and the confluence of the Río Salamá some 900 m. in a 90 km. air-line distance.

Most of the tributaries of the upper river enter from the south, and these have carved basins of considerable size into the northern flanks of the Sierra de Chuacús. Of these, the basins of Sajcabajá, Rabinal-Cubulco, and Salamá (Pl. V, Fig. 1) are the largest. These basins decrease in elevation from west to east, that of Sajcabajá lying at 1250 m., whereas that of Salamá does not exceed 950 m. Bordering these basins on the south is the main crest of the Sierra de Chuacús and Sierra de las Minas, which presents a formidable barrier between the drainages of the Negro to the north and of the Motagua to the south. There are, however, a number of low passes, less than 1500 m. in elevation, through this range. These open into short, steep valleys that plunge down into the Río Motagua. In fact, between Rabinal and Salamá the Chuacús range is considerably lower than to either the east or west, where elevations of 2500 m. are attained.

Paralleling the Río Negro to the south and separated from it by the Sierra de Chuacús, which continues eastward to the Caribbean as the Sierra de las Minas and the Sierra de Mico, is the valley of the Río Motagua. Rising on the Guatemalan Plateau in the vicinity of Santa Cruz Quiché, the Motagua flows eastward to the Caribbean, some 300 km. away. This valley is, in the main, structural in origin. It lies between two ancient masses, the Chuacús-Minas-Mico range to the north and a badly eroded, unnamed ridge (Pl. I, Fig. 2, and Pl. VI, Fig. 1) to the south. Both of these masses were further uplifted during the Pliocene, an event which also rejuvenated the upper course of the Motagua.

The upper third of the valley is of steep gradient and narrow, as may be judged by the fact that in the first 120 km. of its course the river falls from 2000 m. at its source to 300 m. at El Rancho. Below this latter point the valley widens, and at Zacapa, 55 km. east of El Rancho, at the confluence of the Río Zacapa, the flood-plain is roughly 20 km. broad. From El Rancho eastward the local relief of the valley decreases, and in the vicinity of Zacapa the river is intrenched in a broad plain. For the most part, this middle section of the valley is covered with a deep mantle of alluvial materials which have been deposited by the main stream in times of flood and by the numerous tributaries which enter the river from the south.

Below Zacapa the river cuts through a local ridge, and the valley narrows. But below Gualán the valley again broadens, and the lower third of the Motagua meanders through a lowland area that is dotted with oxbows and swamps and is extensively inundated during the wet season. My interest lies in the central part of the Motagua Valley between Gualán and El Rancho.

Throughout the entire length of the corridor uplift is still an active process, as is evidenced by the terrace systems along the stream courses (Pl. III, Fig. 1, and Pl. VI, Fig. 1). In many places these terraces are well defined, and except in gorge areas the streams are everywhere well intrenched in ancient flood-plains.

In summarizing the geology of the corridor three points may be made. First, the corridor consists of a series of valleys and basins that have apparently existed since the late Miocene or early Pliocene in a region in which uplift is continuing. Second, though much of the corridor lies below the 1000 m. contour, an important biotic isopleth in northern Central America, elevations of as much as almost 2000 m. separate the three major drainages that are included in the corridor. Third, except for the middle valleys of the Rios Grijalva and Motagua, the corridor at no place presents an extensive dry-land environment. It is, in fact, often restricted to gorges that may be no more than a few hundred yards in width (Pl. III, Fig. 1 and Pl. IV, Fig. 2).

Climate. — Throughout most of its course the corridor may be described as hot and subhumid. Aside from reports from a mere handful of stations, however, there are no very definite data on the climate of the region, and what little is known has been summarized by Ward and Brooks (1936) and by Sapper (1932).

For the most part, the temperature of the corridor lies within the *A* (frost free) boundary of Köppen (1923). With a latitudinal extent of but 2°, and all of it essentially dry, temperature variations within the region are largely a function of altitude. It is indicated that there is an altitudinal decrease in temperatures amounting to about 0.6° (all temperatures herein are given in degrees centigrade) per 100 m. for mean annual temperatures and possibly somewhat less for the mean temperature of the coldest month. As a generalization, therefore, the *A-C* boundary probably lies somewhere in the neighborhood of the 1000 m. contour. Thus, only in the headwater regions of the Grijalva and Negro drainages and through the passes over the mountains that separate the basins of central Guatemala from the valley of the Río Motagua are other than tropical temperatures encountered. In the Mexican section of the corridor the mean annual temperature of Tuxtla Gutiérrez (550 m.) is 24.4° and of Motozintla (1310 m.), 18.9°. Typical stations in Guatemala, Zacapa (180 m.) and Salamá (920 m.), have mean annual temperatures of 26.4° and 22.6°, respectively. The mean temperatures for the coldest month (December or January) for these same four stations are 21.2°, 16.0°, 23.5°, and 19.9°, respectively. The range in temperature between the coldest and warmest months is in the neighborhood of 6°.

Though much of the region falls within the humid boundary of Köppen, it may be pointed out that even these areas lie very close to the *B* boundary and that high relief in many sections and porous soils in others greatly reduce the effectiveness of the rainfall. Sources from which the precipitation of the corridor stems are not of present interest, and it is sufficient to point out that throughout its entire extent the corridor lies within the rain-shadow of the high mountains and plateaus which border it to the north and northeast. The most humid part of the corridor is probably the lower Grijalva Valley, which at Tuxtla Gutiérrez receives almost 900 mm. of rainfall annually. Farther up the valley, at Motozintla, the annual precipitation amounts to no more than 650 mm. The driest known section of the corridor is the middle Motagua Valley where annual rainfall does not exceed 600 mm., but it is not improbable that parts of the gorge of the Río Negro and headwater valleys of the Grijalva in Guatemala receive even less moisture. Throughout the corridor approximately 90 per cent of the precipitation is deposited during the high-sun period.

Thus, though the Grijalva Valley through its middle course lies within the *Aw* climatic type of Köppen below 1000 m. and probably *Cw* above that level, it is all very close to the *B* boundary. The same may be said of the upland basins of central Guatemala. All of the middle valley of the Río Motagua may be classified as *BS*, and it is not improbable that when data are available, the upper courses of the Grijalva and the Negro will prove to be *BW*.

Vegetation. — Among the various authors who have described or mapped the vegetation of regions through which the corridor passes there seems to be little agreement. From personal experience I am inclined to accept the work of Miranda (1952) on the Grijalva section and those of Steyermark (1950) and Sapper (1894) on the Guatemalan section as the most reliable.

Miranda mapped the floor of the Central Depression of Chiapas as basically savanna throughout its length. This does not imply that the valley consists of an unbroken grassland. Indeed, much of the valley supports stands of low dry forest, patches of mesquite-like thickets, occasional stands of palms, and, along the water courses, gallery forest. Where savanna does occur, the grassy plains are dotted with stunted trees, which may occur singly or in small groves (Pl. II, Fig. 1). In the upper parts of the valley a cover of low shrubs and small trees, largely acacias, is not uncommon (Pl. II, Fig. 2). These may form impenetrable thickets or, more often, may be scattered over the grasslands to produce a more open brushland. The forests of low, deciduous trees, rarely over 10 m. in height, are especially common in the upper end of the depression. These forest groves, though appearing to be dense jungle from without, are, in reality, fairly open with little undergrowth and with a deep mantle of dry leaves on the forest floor. Palm groves are extremely local. Along the major water courses a narrow strip of gallery forest may generally be found. Inasmuch as the majority of the streams are deeply intrenched, this type of forest is restricted to the steep river banks and breaks off sharply at the edge of the higher land.

The main slopes of the depression and higher ridges within the valley support, in the main, dry forests and brushland. At higher levels (above about 1000 m.) oak makes its appearance, and pine is not uncommon on the crests of the ridges.

Generally speaking, the greater part of the valley is devoted to the grazing industry. Clearing of the land and firing have destroyed considerable virgin cover, and planted pasturage not infrequently obscures the virgin condition. But taken as a unit, the vegetation of the Central Depression all points toward subhumid conditions.

The headwater valleys of the Grijalva system support a vegetation cover that is almost desert in aspect. At Canibal the valley floor was without a continuous sod cover (Pl. III, Fig. 1). Dense thickets of mesquite and other xeric shrubs and an abundance of *Cereus*-like cacti and prickly pears form a cover that is known as *espinal* (Pl. III, Fig. 2). Even gallery forest was lacking along the water courses. The steep valley slopes support a rank growth of desert shrubs and stunted trees (Pl. III, Fig. 2) which, above the 1300 m. contour, shades into pine and oak.

The highlands in the vicinity of Huehuetenango which form the divide between the Grijalva and Negro drainages lie within the oak-pine belt (Pl. IV, Fig. 1). For the most part, the forests of this region are open, with little underbrush, and lack continuity. Possibly owing to long occupation by Indians and Europeans who may have cleared much of the forest land, there are, in the region, extensive stretches of steppe grasslands.

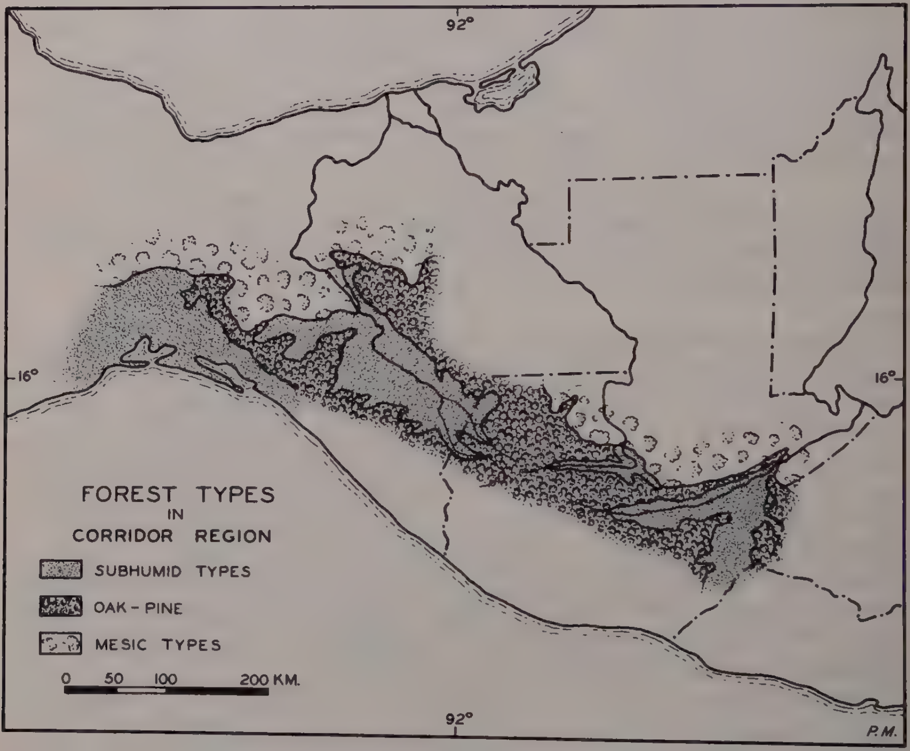
Upon entering the valley of the Río Negro at Sacapulas one encounters a vegetation cover that is in most respects similar to that of the Cuilco region. I am unfamiliar with the gorge down to the entrance of the Río Salamá, but Sapper mapped it as grass and shrub steppe with chaparral and *Cereus*-form cacti. In the region of Chixoy, well below the entrance of the Salamá, the character of the vegetation is somewhat more mesic (Pl. IV, Fig. 2), but there is little reason to suspect that any more humid types occur between Sacapulas and the point at which the Negro enters the lowlands of the Yucatán Peninsula. Throughout this region the oak-pine belt on the upper valley slopes extends somewhat farther down than at Canibal. At La Primavera, for instance, one encounters open oak and pine forests at about the 1000 m. level.

Depending upon elevation, the basins that drain northward into the Río Negro support varied types of cover. The highest and most westerly, that of Sacabajá, may be classified as a pine-savanna. For the most part, a cover of tall savanna grasses features the basin, and the pine occurs in open groves. Along the water courses a narrow band of open broadleaf forest may be present. The Rabinal-Cubulco Basin, the middle of the three major basins, is much like that of Sacabajá in the west, but in the east a cover of short grasses and dry-land shrubs takes over. The most easterly and the lowest, the Salamá Basin, is steppe land with low, dry-land shrubs and many varieties of small cacti (Pl. V, Fig. 1). As it is relatively intensively cultivated, there is difficulty in judging just what primeval conditions were. In all instances the mountain slopes above the basins support a cover of pine and oak at elevations up to about 1500 m. (Pl. V, Fig. 2), where the cloud forest begins.

Between the basins of central Guatemala and the Motagua Valley the massive Sierra de Chuacús supports on its north side a cloud forest above the 1500 m. contour, but on its south (lee) slopes this wet forest type is not encountered lower than about 2000 m. Below those levels oak and pine form the dominant cover. The latter forests are fairly open but provide a somewhat mesic environment. In the region under discussion the mountains, as previously noted, break down somewhat, and much of the crest to the south of the basins lies below the cloud-forest level. On the south slopes of the range oak and pine predominate down to about the 1000 m. level, below which desert shrubs form a dense tangle. The desert landscape of the Motagua Valley is not encountered until one descends to roughly the 500 m. level.

The vegetation of the middle Motagua Valley has been classified as "desert-chaparral" by Steyermark, a term that he applied also to vegetation of the Río Negro gorge. Perhaps the most striking feature of the cover is the abundance of the large, *Cereus*-like cacti (Pl. VI, Fig. 2). Depending upon relief, water table, and other physical features, there is considerable variation in the cover of this part of the valley. Rocky knolls support rank growths of spiny desert shrubs and cacti; more level plains may resemble short-grass steppe lands with scattered low trees of the acacia type or extensive thickets of mesquite (Pl. VI, Fig. 2); intermittent stream courses are lined with stunted deciduous trees, shrubs, and dense stands of cacti; whereas along permanent water courses a narrow band of gallery forest may prevail. Toward the west, as the uplands of the plateau are approached, the desert landscape gives way to dry brushland and oak forests, and to the east toward the Caribbean lowlands, where conditions become more mesic, the desert landscape shades gradually into the wet forest of the lower valley. Gualán appears to serve as a suitable boundary limiting the eastward extent of the desert.

Thus, throughout the entire extent of the corridor from the Isthmus of Tehuantepec to the Motagua Desert an essentially xeric type of cover prevails. Even where forests do occur, with the exception of the gallery forests that may border larger streams, they are of types which are characteristic of subhumid lands. Map 2 shows the distribution of the major vegetation formations in the corridor region.



Map 2

HERPETOFAUNAL INDICATORS OF THE CORRIDOR

It is not within the bounds of this paper to discuss the herpetofauna of the dry-land corridor in its entirety. Indeed, no part of the corridor is known in sufficient detail to permit such a discussion. Smith (1946) has commented briefly on a collection of reptiles and amphibians from the middle Grijalva Valley, and Schmidt and Stuart (1941) have given a short account of the herpetofauna of the Salamá Basin. Other than the data in these two works, our present knowledge of the fauna of the corridor is drawn from scattered collections from miscellaneous stations which have yielded only the commoner species of the various areas.

A study of these collections reveals the fact that there is little unity in the herpetofauna of the corridor as a whole. The fauna of any one station does, it is true, contain certain forms which seem to be generally distributed throughout the dry-lands of northern Central America and southern Mexico, but the fauna of any single station is often characterized by the presence of species that are more frequently components of adjacent biotic areas than of the corridor itself. Thus, were one to compare the list of species known from the middle valley of the Río Motagua with the list presented by Smith for the middle Grijalva Valley, one would find little in common in the two areas. Furthermore, the rarities upon which faunal similarities and dissimilarities are so often based have not as yet been secured in the haphazard collecting that has characterized field investigations in the corridor.

Any suggestion of continuity in the fauna of the corridor must stem, therefore, from certain species that occur abundantly in their respective habitats and which are not apt to be overlooked by even the most casual collector. It is, in fact, through an analysis of certain forms of high productivity that the biological importance of the corridor is best illustrated. Some of the forms, therefore, that I consider sufficiently well known to serve as "indicators" will be briefly examined.

Hypopachus championi Stuart

Described from the Salamá Basin, this species has since been found to be widely distributed over the southeastern uplands of Guatemala. Insofar as is known, its vertical limits are relatively narrow. To date it has not been secured at elevations below 900 m. nor above 1500 m. Indeed, over most of Guatemala it is replaced by some member of the *inguinalis* group above the latter elevation. It appears, therefore, to be confined to the upper parts of the savanna and desert-shrub environment and to the lower parts of the oak or oak-pine zone.

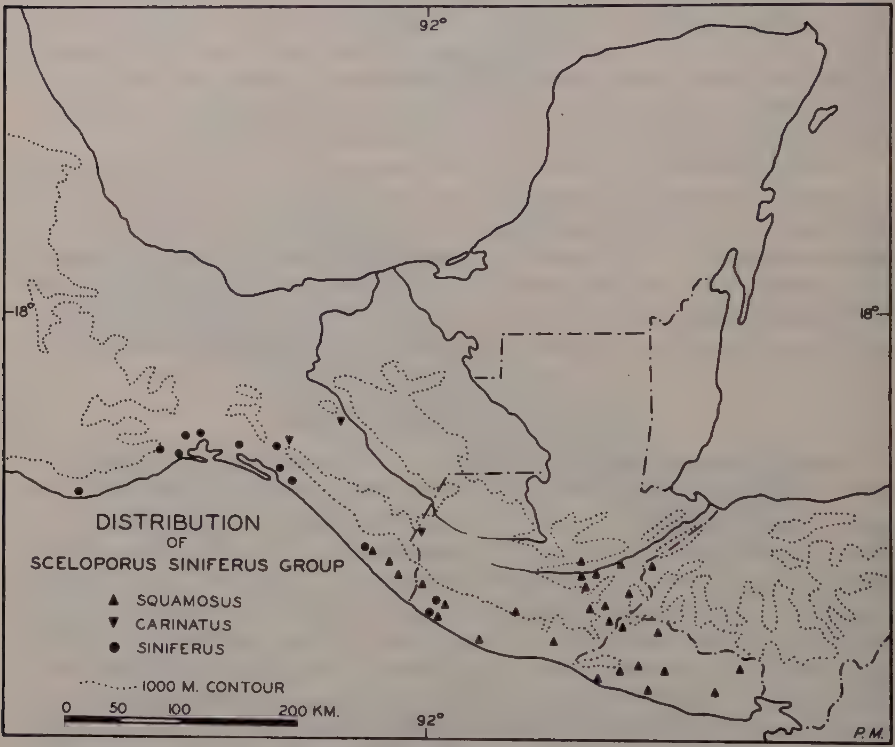
Though a member of a lowland group, it is not a subspecies of *cuneus*, which is widely distributed over the lowlands of the Caribbean versant of northern Central America and Mexico and also appears in the United States. It is most closely related, rather, to *Hypopachus maculatus* Taylor, which is known only from the middle Grijalva Valley. The genus is unknown from the Pacific versant south of the Isthmus of Tehuantepec.

These two closely related forms, *H. championi* and *H. maculatus*, though now lying at either end of the corridor and failing to contact each other geographically, strongly suggest previous continuity.

Sceloporus, siniferus group
(Map 3)

This small group of scelopori is distributed from Guerrero southward to Nicaragua. With the exception of a small population of *squamosus* in central Guatemala and in northern Honduras, the group is essentially one that is distributed along the Pacific versant of southern Mexico and Central America.

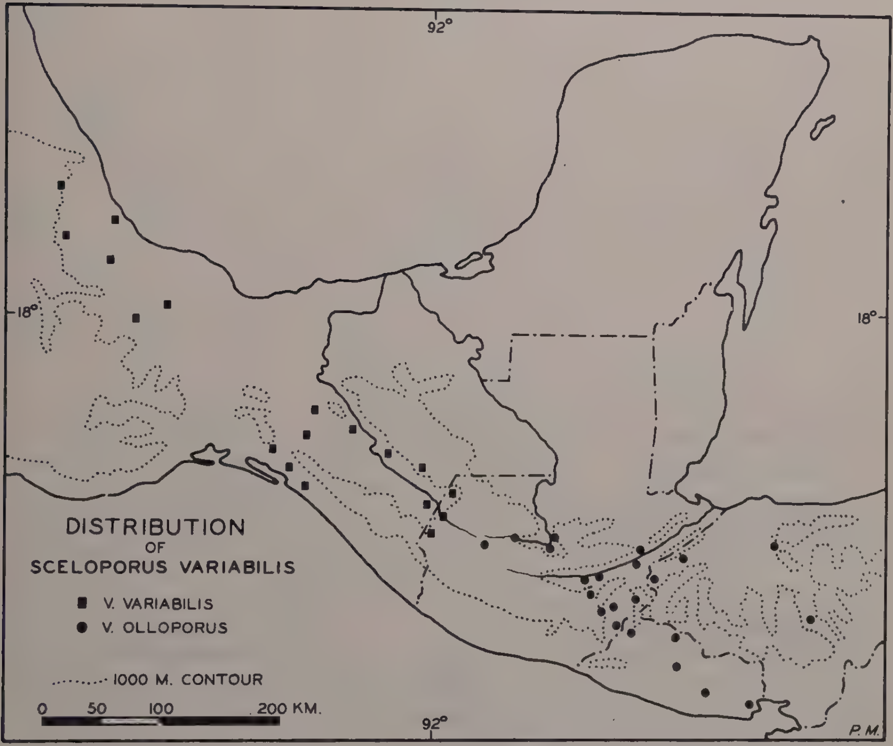
Smith (1939: 300-302), though admitting close affinity between *squamosus* and *carinatus*, gave a somewhat ambiguous presentation of the specific interrelationships of the group. Excluding *ochoterenae*, which is but remotely related to other members of the group, the remaining four species appear to be contained in two subgroups, i. e., *siniferus* and *cupreus*, as opposed to *carinatus* and *squamosus*. The former two are distributed along the Pacific versant from Guerrero to western Guatemala. The latter two extend from the western end of the Grijalva Valley through the dry-land corridor to the Motagua Valley and thence southward across the southeastern uplands of Guatemala to the Pacific versant along which *squamosus* is distributed from eastern Chiapas to Nicaragua.



Map 3

On the basis of available data it would appear that from a prototypic population a "*siniferus*" division split off in one direction and a "*carinatus*" division in another. From the former developed the modern *siniferus* and *cupreus*, and from the latter *carinatus* and *squamosus*. This final stage in the evolution of the modern forms probably took place *in situ*. At any rate, the overlap in the ranges of *siniferus* and *squamosus* in western Guatemala and eastern Chiapas suggests fairly remote relationships between the two.

Thus, in the absence of extent continuity, through their obvious phylogenetic relationship suggesting previous geographic continuity, *S. carinatus* and *S. squamosus* parallel the situation observed in *H. championi* and *H. maculatus*.



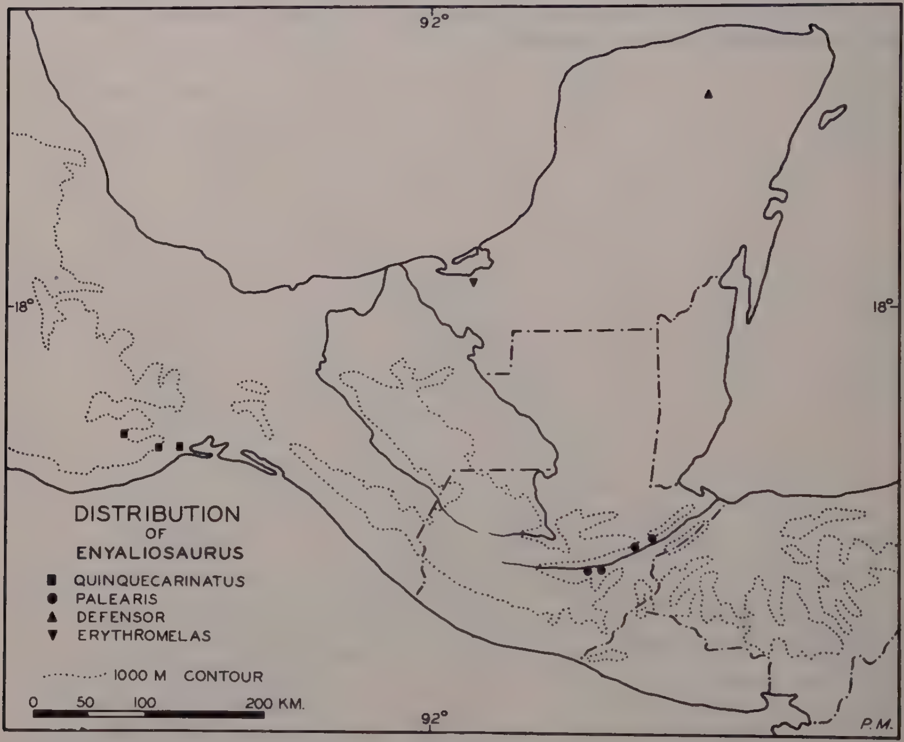
Map 4

Sceloporus variabilis subspp.
(Map 4)

This species ranging from Texas to Costa Rica includes about a half-dozen subspecies of which only two, *variabilis variabilis* and *variabilis olloporus*, are factors in the problem at hand. The typical form extends from southern Tamaulipas southward along the coastal plain of the Gulf of Mexico and the eastern side of the Mexican Plateau across the Tehuantepec isthmian region and into the Grijalva (Cuilco) Valley in southwestern Guatemala. It is known from sea level to at least 1900 m. elevation. In southwestern Guatemala (Canibal) it appears to intergrade with *olloporus*.

This latter form occurs through the dry-lands of central Guatemala southward to Costa Rica. It has been taken from near sea level to an elevation of 2200 m. South of southeastern Guatemala and north-central Honduras it appears to be restricted to the Pacific versant.

It is important to note that no form of the subspecies is known from the Pacific versant from the Isthmus of Tehuantepec at least as far south as El Salvador. The *variabilis* group is represented on the Caribbean versant from southern Veracruz to Honduras (i. e., the lowlands of the Yucatán Peninsula) by two species, *cozumelae* and *teapensis*, neither of which is particularly closely related to either *variabilis* or *olloporus* even though placed by Smith (1939) in the same group.

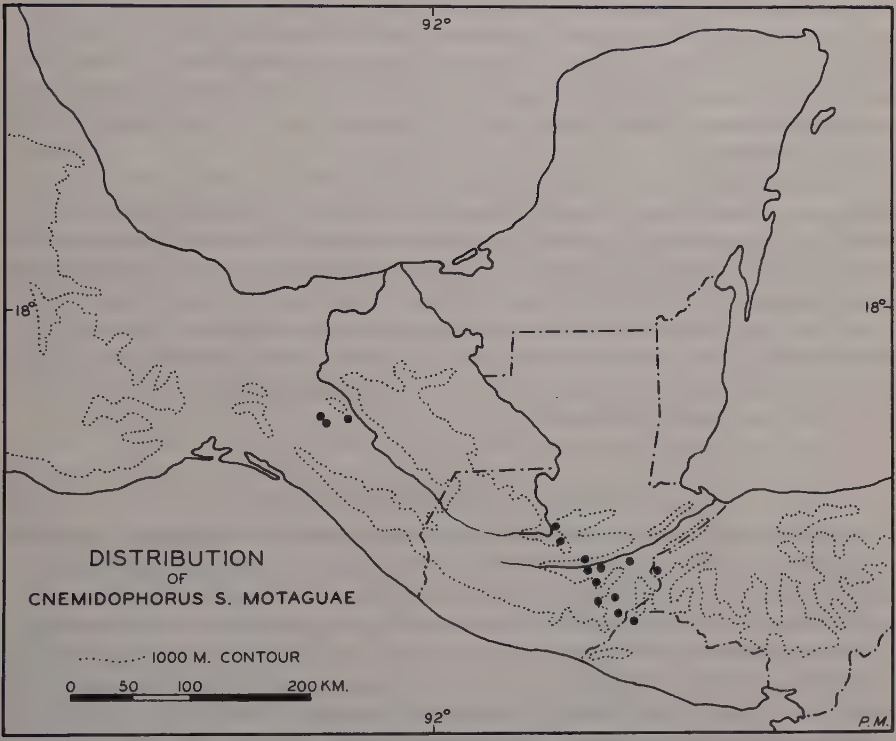


Map 5

Such gaps in the distribution of these two forms as appear on the map are indicative only of insufficient collecting. In attaining elevations of 2200 m. it is evident that the two find no barriers throughout the length of the corridor. Their geographic continuity is the most complete of any form found in the corridor.

Enyaliosaurus spp.
(Map 5)

All geographic data suggest that *Enyaliosaurus* is a relict genus. Only five forms are known, and these appear to be divided among two groups. One, occupying the outer end of the Yucatán Peninsula, is composed of *defensor* and *erythromelas*. The other, which is of present interest, contains *clarki* in Michoacán, *quinquecarinatus* of southern Oaxaca, and *palearis* from the Motagua Valley. All members of the genus are lowlanders and are unknown from elevations above 500 m. Though separated by the entire lengths of the Grijalva and Negro valleys and by the interior basins of central Guatemala, there can be no question as to the very close genetic affinities of *palearis* and *quinquecarinatus*. Previous geographic continuity through the corridor will be shown to be the best explanation of the extant condition.



Map 6

Cnemidophorus sacki motaguae Sackett
(Map 6)

The status of this form is still somewhat problematic. Smith and Taylor (1950: 181) considered *motaguae* a synonym of *bocourti*. With this conclusion I do not agree. From the scanty material available from Oaxaca and the abundant material available from Chiapas and Guatemala, it seems fairly certain that the former has a much lower femoral pore count than the latter. I am inclined, therefore, to retain the name *motaguae* for populations south of the Isthmus of Tehuantepec and to restrict the name *bocourti* to those occurring north of the Isthmus.

Cnemidophorus sacki motaguae shows considerable discontinuity in its range. Known from the vicinity of Tuxtla Gutiérrez in the middle Grijalva Valley, it does not make an appearance again until it is encountered in the gorge of the Río Negro and the Salamá Basin of central Guatemala. Throughout the middle valley of the Río Motagua and over the southeastern uplands of Guatemala it is abundant up to an elevation of about 1000 m. Though I have made an intensive search for it at elevations near the 1000 m. contour in the upper valley of the Grijalva and in the Cuilco Valley, I have not encountered it in those regions. At no place between Tehuantepec and El Salvador does it occur along the Pacific versant.

Aside from *bocourti* and possibly other forms farther to the north, *motaguae*, though only one of a number of races of *sacki*, appears to have no immediate affinities in southern Mexico. Certainly,it seems to have little in common with *angusticeps* from the outer end of the Yucatán Peninsula. No other representative of the *sacki* group is known from the lowlands of the Yucatán Peninsula to the south of the subhumid outer parts of the peninsula. This form, though undifferentiated at either end of the corridor, displays a geographic pattern similar to that obtaining in *Enyaliosaurus*.

Leptodeira rhombifera Günther

Though the following may further confuse an already badly confused concept of *Leptodeira rhombifera* and *L. maculata* (Hallowell), it is, nevertheless, necessary to present here some thoughts I have had for some time which are of pertinence not only as concerns the desert corridor but also concerning the relationships of these two species. Dunn (1936) considered *maculata* a race of *septentrionalis* and accorded full specific status to *rhombifera*. The only characters he presented for the separation of the two were (1) the presence of a dark nape stripe in *rhombifera* and the absence of the same in *maculata*, and (2) the more ventral extension of the dorsal rhombs in *maculata* as compared with *rhombifera*. Taylor (1938: 337-42) has shown this last character to be variable in *maculata* and hence untenable as a character for the separation of the two forms. He has shown further that *maculata* and *septentrionalis* are distinct species with overlapping ranges, and other of his data suggest that *maculata* may be vicariously represented by subspecies in various parts of its extensive range. He did not consider *rhombifera* since that form does not occur in Mexico.

Geographically, *maculata* presents a really difficult problem. Although the type was described from Tahiti, it is now generally agreed that it could not have originated from that island. Various suggestions attribute it to Costa Rica or, more probably, to Nicaragua. The type of *maculata* is said to possess a single preocular and possibly one postocular. Taylor (1938) stated that two preoculars are almost invariable in the Mexican form now known as *maculata*, as is true in all of the large series of *rhombifera* known to me. Two postoculars are invariable in *maculata*, and, though I have seen occasional *rhombifera* with three, I have no record of any specimen with only one. Aside from the type and a series of six specimens in the Museo Nacional de Costa Rica which are merely presumed to have stemmed from that country, rather extensive collecting has failed to reveal *maculata* south of San Ricardo in the Grijalva Valley and Tonolá, Chiapas, on the Pacific versant. Taylor (1951: 126) hesitated to accept Costa Rica as the source of the six *maculata* in the Costa Rican museum, and I certainly concur with his opinion. These facts, it seems to me, argue that either the *maculata* of Hallowell is not the form to which that name is currently applied, or the type did not stem from lower Central America.

The very close resemblance of *maculata* to *rhombifera* suggests genetic relationship between the two. Apparently, only the nape stripe presents a diagnostic character for separation, and Taylor (1938: 341) noted that a specimen identified as *maculata* and stemming from Asunción, Chiapas (Grijalva Valley), actually has the nape stripe characteristic of *rhombifera*. In my opinion, the two belong to the same species group, and I would not be surprised if future investigation were to prove them to be subspecies.

Leptodeira rhombifera is known from the dry interior valleys of Central Guatemala southward across the southeastern highlands of Guatemala and along the Pacific versant from extreme eastern Guatemala to Panama. It is unknown from the wetter parts of the Pacific versant of eastern Chiapas and western Guatemala, collecting in both regions having been quite thorough. Neither is it known from the lowlands of the Yucatán Peninsula. Throughout its range it is unknown from elevations above 1000 m.; thus, *maculata* and *rhombifera* have distributions not very different from those of *Sceloporus variabilis variabilis* and *olloporus*.

Though the six groups given above constitute the best herpetological indicators of the corridor, there are several other forms which, though still too imperfectly known to be definitely assigned to this scheme, possess suggestive distributions. Most striking is the distribution of the *pulcher* group of *Conophis*. The typical form, *pulcher pulcher*, though described from "Verapaz, near the Petén" in Guatemala, has since been taken only at Canibal, El Rancho, and Progreso, all within the corridor. This suggests that the form is a dry-land inhabitant and that the types may possibly have originated from the Chisec savannas in northern Alta Verapaz. It has never been taken in a mesic environment. The subspecies *plagosus* is known only from the Pacific versant from eastern Chiapas to El Salvador. There is the possibility, therefore, that the typical form may have passed through the corridor from the chain of savannas that extends from the central part of the Yucatán lowlands into Veracruz, Mexico, or it may have entered the corridor via the Motagua Valley. In either case only the corridor seems to offer an explanation of its occurrence in the middle Motagua Valley and the upper Grijalva Valley. It will probably be shown to be in contact with *plagosus* across the southeastern highlands of Guatemala.

No less suggestive is the distribution of a chain of *Bufo coccifer*-like toads. Typical *coccifer* appears to range from Costa Rica northward into the southeastern highlands of Guatemala. In central Guatemala, at intermediate elevations, it is replaced by an undescribed but obviously related form, and in Guerrero and the Tehuantepec region of Mexico another undescribed but related form occurs. No *coccifer*-like species is known from either the lowlands of the Yucatán Peninsula or the Pacific versant of Guatemala and Chiapas. Again, dispersal through the corridor is indicated.

Aside from the indicator and "near indicator" forms, the herpetofauna of the corridor region is anything but spectacular. Collections to date have revealed that, for the most part, this subhumid area supports at best an impoverished assemblage of wide-ranging xeric types. Some of the more conspicuous of these are *Leptotyphlops phenops phenops*, *Masticophis mentovarius mentovarius*, *Oxybelis aeneus* subsp., *Stenorrhina freminvillei*, *Crotalus durrisus durrisus* among the snakes and *Ctenosaura similis similis*, *Cnemidophorus deppei deppei*, and *Ameiva undulata* subsp. among the lizards.

It may be of some significance that no mesic types are known from the corridor region even though patches of gallery forest not too far removed from humid environments are present, i. e., the gallery forest of the middle Motagua Valley. This would seem to suggest that such mesic conditions are too small and have been too long isolated to support even relict populations of wet-forest forms.

In summarizing the distribution and affinities of the indicators and "near indicators" discussed, several pertinent points must be brought out. First, geographic continuity throughout the length of the corridor can be definitely proved in only one instance. Of the remaining species only *Hypopachus championi* and the *Bufo coccifer* series attain sufficiently high elevations in the oak-pine zone of Guatemala to suggest that they may occur continuously above the dry valleys proper. All the other indicator forms are essentially lowland types, so that geographic continuity in their ranges through the corridor seems improbable.

Second, the closest genetic affinities of the corridor indicators in Guatemala occur not on the lowlands of the Caribbean to the north and east nor on those of the Pacific to the south and west, but rather in lowland areas to the north of the Isthmus of Tehuantepec or along the moderately elevated uplands of Nuclear Central America and along the Pacific lowlands southward. In some instances the same form extends from western Chiapas through the corridor and then southward at least into El Salvador, e.g., *Cnemidophorus sacki motaguae*, which is represented by *Cnemidophorus sacki bocourti* north of the Isthmus of

Tehuantepec. *Sceloporus variabilis* shows much the same pattern except that the typical form extends northward into Tamaulipas, but *olloporus* continues southward into Costa Rica along the Pacific versant. The affinities of *Enyaliosaurus palearis,* as indicated, are not the forms occurring on the Yucatán Peninsula, but, rather, *quinquecarinatus* and *clarki* of Tehuantepec and Guerrero, respectively.

Third, there appears to be no consistency in the differentiation levels in the various populations of the indicator forms in the corridor. It has been noted that *Cnemidophorus sacki motaguae,* though discontinuous in its distribution, has remained undifferentiated throughout the length of the corridor. In contrast, *Sceloporus variabilis,* continuous in its distribution, has split into different races on either side of the main break in the corridor in the Huehuetenango region; *Sceloporus carinatus* and *Sceloporus squamosus,* noncontinuous in their ranges, have differentiated to the specific level.

DISCUSSION

In the Introduction it was noted that a search for a subhumid corridor through northern Central America was initiated by observation of extremely tenuous continuities or discontinuities in the geographic distribution of certain herpetological elements that are essentially dry-land inhabitants. I am concerned, therefore, with the "how," "when," and "where" these conditions were brought about. Three possibilities present themselves. First, there may have been, in the past, continuity in the ranges of certain species through the lowlands of the Yucatán Peninsula. Second, a dry-land corridor may have previously existed along the Pacific versant of northern Central America. And third, the only pathway for dispersal southward for certain dry-land forms (most evidence points to a dispersal from north to south) has been and remains the corridor described herein. To these suggestions may be added the probability of convergent evolution in populations at either end of the corridor, an explanation which, to use the vernacular, would be "making it the hard way."

A route through the lowlands of the Yucatán Peninsula from the Isthmus of Tehuantepec to the middle Motagua Valley would postulate the occurrence of conditions far more xeric than those existing today. True, a chain of savannas from the Veracruz region of Mexico into central El Petén is extant, but as the eastern seaboard is approached these savannas give way to the very wet forests of the eastern parts of the Yucatán Peninsula and of Alta Verapaz. Furthermore, both Ruthven (1912) and Stuart (1935) have given reasons for considering these savannas to be of relatively recent origin. It cannot be doubted, however, that savanna chains similar to those now in existence have at various times wound through the forests of the Yucatán lowlands, if one is to explain certain elements that now occur as isolated populations in local savanna and dry-forest areas on the lowlands. Had the corridor indicators previously made use of such pathways, however, it might well be expected that they or at least their very closest affinities would be present today in such areas. This has been shown to be contrary to fact.

A very similar argument against a Pacific versant corridor obtains. Along the Pacific lowlands from central Chiapas into about central Guatemala mesic conditions occur. To the north and to the south of these two points, respectively, the environment becomes increasingly drier. This mesic region has apparently acted as a barrier to the free movement of a number of forms along the Pacific lowlands, and it is in this general area that a faunal break occurs. A discussion of this point will be presented by me in a forthcoming account of the herpetofauna of the Pacific versant of Guatemala. Of the several indicator species *Sceloporous squamosus* and its relative *Sceloporus carinatus* come closest to completing a distribution circle through the corridor, around the Mexican Sierra Madre to the north, the Guatemalan highlands to the south, and along the Pacific versant. Had previous continuity in the ranges of *carinatus* and *squamosus* existed along the Pacific lowlands, it would certainly be necessary to postulate far more xeric conditions in the past than exist now. As will be shown, such a postulate seems highly improbable.

Only the corridor is left, then, to serve as a pathway for the dispersal of the indicators mentioned. Insofar as the indicators are concerned, all evidence seems to point to a dispersal from north to south. This evidence is twofold. In the groups that have been studied intensively, especially *Sceloporus* and *Cnemidophorus*, there can be little doubt that genetic relationships of the corridor forms center either in the Tehuantepec isthmian region or farther north on the Mexican Plateau. Ecologically, moreover, all the indicators belong to groups that are essentially dry-land types. Suitable environments for these are abundant north of the Isthmus of Tehuantepec but are rare and most probably of relatively recent origin to the south.

To account for the present-day discontinuity in the ranges of the indicators, it seems hardly necessary to go back any further than the Pliocene, during which, from all available evidence, the corridor began its history. The guarded statements of Olsen and McGrew (1941) lead one to believe that northern Central America during the lower Pliocene was probably a rolling upland, fairly warm and humid, and supporting a cover of rain forest and scattered grasslands or forest-margin vegetation. The orogenic movements of the Pliocene which changed the topography of all of northern Central America initiated the development of the corridor. The rising of the Mesa Central of Chiapas, the Sierra de los Cuchumatanes, the highlands of Alta Verapaz, and the Chuacús - Minas-Mico range of Guatemala certainly must have produced rain-shadow conditions in the corridor at a fairly early date. As the highlands increased in elevation to the present time (indeed uplift continues) this rain- shadow condition must have become more and more intense. Though it is certain that there were periods of dry conditions at various times during the Pleistocene, there are no data to indicate that northern Central America was at any time drier than it is today. Certainly, any pronounced aridity would have brought about extinction of the many ancient, mesic amphibian and reptilian types that are now so conspicuous a feature of the herpetofauna of the lowlands of the Yucatán Peninsula. Indeed, if the Sangamon may be taken as an indicator of conditions during interglacial stages, a climate even more mesic than that of today probably existed in that region (Hibbard, 1952, and van der Schalie, 1953). In the corridor region, however, the high mountain barriers between it and the sources of moisture must have ensured continuously xeric conditions.

Thus, it is indicated that dry-land types probably entered the corridor shortly after its formation had begun. As uplift continued, first one species and then another was broken into populations isolated one from another by highland breaks in the corridor.

The several differentiation levels that are now encountered in the indicators have resulted from internal factors of the animals themselves, especially temperature and humidity tolerances, motility, and fecundity. Thus, *Enyaliosaurus*, restricted to elevations below about 500 m. and to the most xeric environments, was the first to be divided into isolated populations which differentiated to the specific level, i. e., *palearis* in the middle Motagua Valley and *quinquecarinatus* on the Pacific side of the Isthmus of Tehuantepec. The prototype of *Sceloporus carinatus* and *squamosus*, apparently tolerant to temperatures of elevations up to 1000 m., would have split somewhat later but still early enough to permit specific differentiation at either end of the corridor. *Cnemidophorus sacki*, though attaining elevations of no more than 1000 m., is representative of a form of high fecundity and of far greater motility (or vagility, if I understand the term) than either *Sceloporus carinatus* or *Sceloporus squamosus* and has remained undifferentiated in the corridor region. *Sceloporus variabilis*, though probably continuous in its distribution, is possessed of rather low vagility, and distance alone appears to have enhanced subspecific differentiation at either end of the corridor. *Hypopachus*, though ranging into relatively high elevations, has similarly been effected by distance and by its short period of activity during the breeding season. It is represented by different species, *maculatus* and *championi*, at either end of the corridor.

On the other hand, it is difficult to explain why certain species have not made use of the corridor. For instance, *Conophis vittatus*, though recorded from the Grijalva Valley, has not managed to invade the corridor in Guatemala. It is entirely possible that other elements will fit into the situation outlined above once the corridor has been more thoroughly studied and the relationships of many forms are better understood.

To what extent other groups of animals have made use of this corridor is at present unknown. The fact remains, however, that a subhumid environment of considerable age linking the dry-lands of southern Mexico with those of northern Central America has been available. If essentially dry-land types in other animal groups show geographic discontinuity or near discontinuity through Guatemala, Honduras, El Salvador, and farther south, it is feasible to assume that they have made use of the corridor in the absence of suitable environments along either the Pacific or Caribbean mesic lowlands.

SUMMARY

Observed discontinuities in the distribution of certain amphibians and reptiles through the dry-lands of southern Mexico and central and eastern Guatemala led me to search for a subhumid corridor between the the Isthmus of Tehuantepec and the deserts of eastern Guatemala and northern Honduras.

Such a corridor was found through the valley of the Río Grijalva of Chiapas and those of the Negro and Motagua of Guatemala. This corridor is comprised of valleys lying for the most part below an elevation of 1000 m. but broken by divides that may attain a height of 2000 m. It is indicated that the corridor had its origin during the Pliocene when the major topographic features of the valleys were outlined and their subhumid climatic conditions were initiated. At present its vegetation cover varies from savanna to desert shrub but in no part could it be termed mesic.

It is believed that herpetological indicators such as certain closely related species, subspecies, or populations in the genera *Hypopachus*, *Sceloporus*, *Enyaliosaurus*, *Cnemidophorus*, and *Leptodeira* could have reached the subhumid lands of Honduras, Guatemala, and the Pacific versant of lower Central America only through this corridor. The absence of closely related forms and the presumedly continuously mesic environments on the lowlands of the Pacific and Caribbean versants between the Isthmus of Tehuantepec and southeastern Guatemala argue against migrations of dry-land forms through those lowland areas.

The biogeographic implications of this subhumid corridor are still extremely vague. Further explanation of the various differentiation levels attained by herpetological elements at either end of the corridor must be sought, and the reasons for the inability of many other groups to have made use of the corridor must be given consideration.

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Copies of this contribution may be purchased from the University of Michigan Press, Ann Arbor, Michigan. Price, $ 0.75.

PLATES

PLATE I

FIG. 1. Vegetation on the Pacific side of the Isthmus of Tehuantepec near the village of Tehuantepec. This xeric cover is more or less typical of the greater part of the Plains of Tehuantepec, where grazing is the main industry. It is widespread over much of the Pacific versant of southern Mexico and is representative of the environment obtaining at the northern end of the subhumid corridor. The thickets of mesquite with occasional stunted trees are often so dense that penetration is possible only along cattle trails. February, 1953; elevation, about 55 m.

FIG. 2. Subhumid uplands in the vicinity of San Pedro Pinula, Guatemala (about 30 air-line km. slightly east of south of El Rancho). This environment type is typical of the southeastern highlands of Guatemala below about 1000 m. and at the southern end of the corridor. A number of species undoubtedly moved across these uplands from the Motagua Valley or vice versa to attain the drier environments of the Pacific versant of lower Central America. The hills in the background support a cover of oak and pine which is the vegetation type of elevations between about 1000 and 2000 m. over most of the southeastern uplands. These hills represent the remnants of the ancient mountain mass that forms the southern slopes of the Motagua Valley. March, 1952; elevation, about 1000 m.

PLATE I

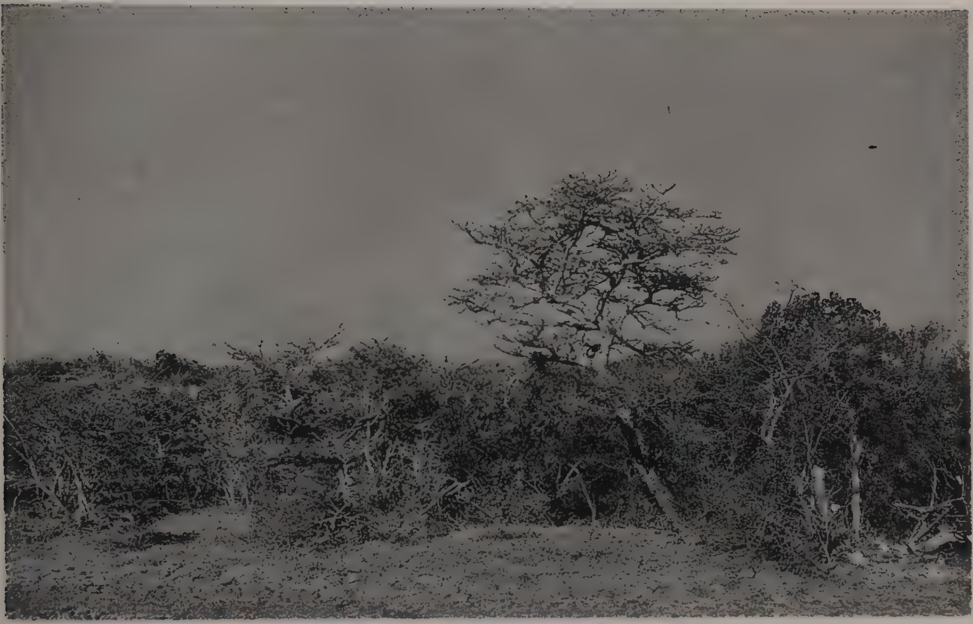

Fig. 1

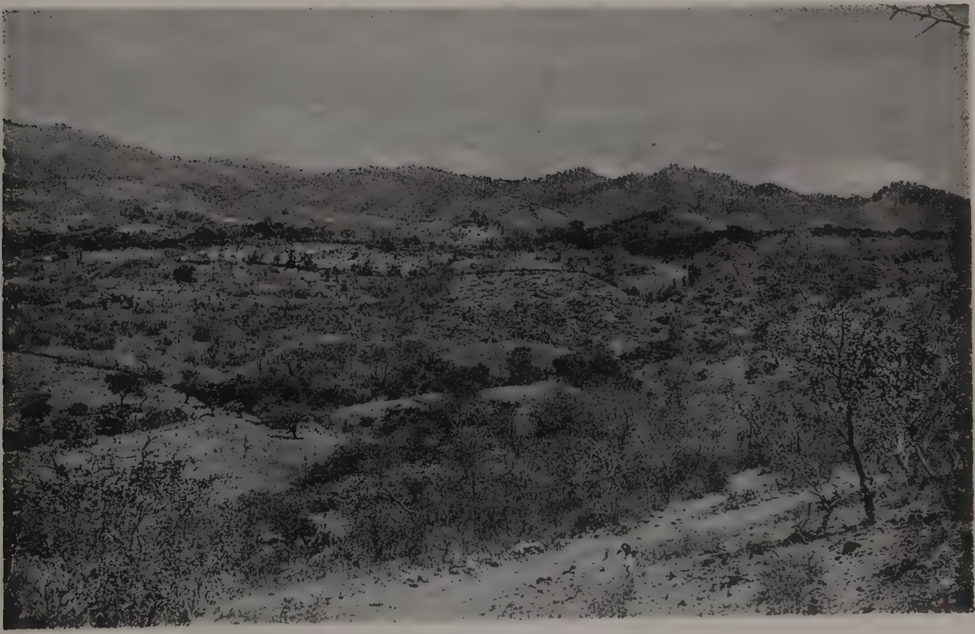

Fig. 2

PLATE II

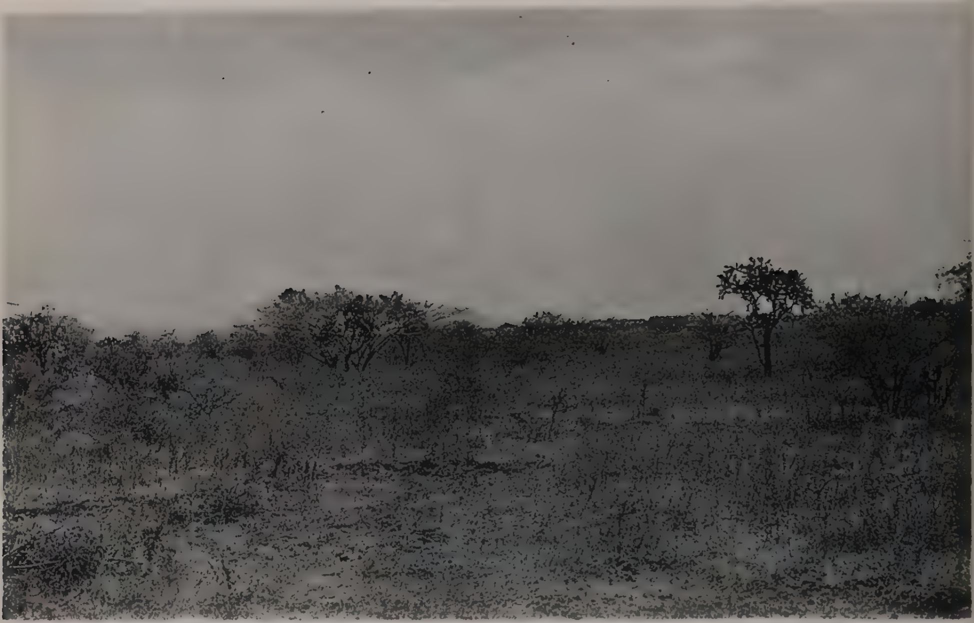

FIG. 1

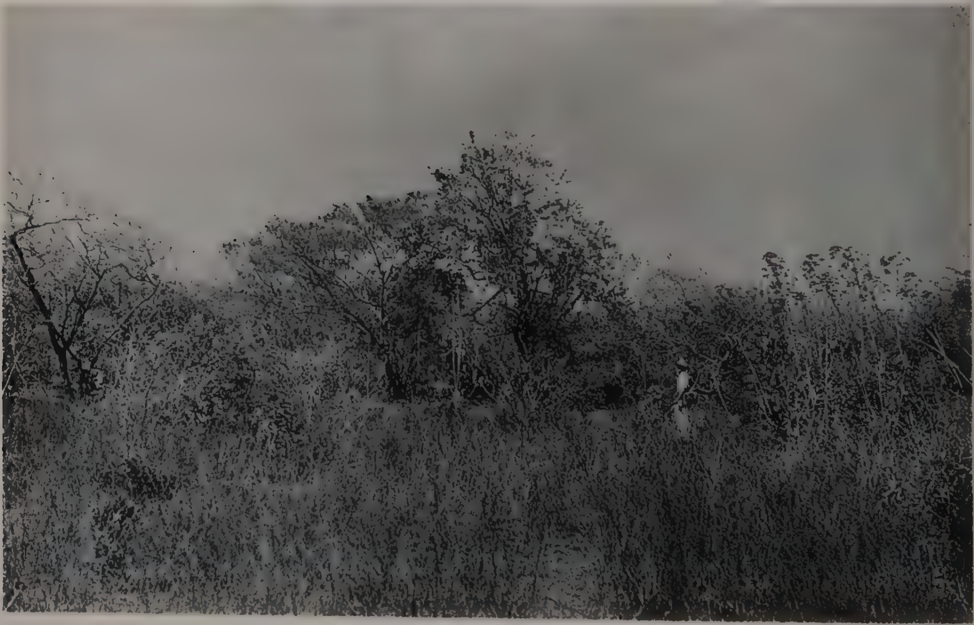

FIG. 2

PLATE II

FIG. 1. Grassy savannas with scattered *nance*, *jicaro*, and cacti in the vicinity of Ocozocoautla in the middle Grijalva Valley. Savannas such as these are the most common vegetation type in the Ocozocoautla-Tuxtla Gutiérrez region. In the left background is the outline of the north face of the outliers of the Sierra Madre. Much of the middle valley of the Grijalva is of considerably higher relief. February, 1953; elevation, about 600 m.

FIG. 2. Savanna and low scrub forest in the upper Grijalva Valley not far from the Guatemalan border and only a few hundred yards from the Río San Gregório. Primarily cattle country, the land is frequently burned over, and the vegetation, though essentially the same as that encountered on the Tehuantepec Plains, is much less dense. February, 1953; elevation, about 800 m.

PLATE III

FIG. 1. Valley of the Río Cuilco (looking downstream) at Canibal on the Mexican border. Note particularly the sparse vegetation on the valley slopes. On the left bank of the stream are groves of planted mango and citrus fruits. Only a single terrace, that on the right bank, is visible, though there are three on the left bank farther upstream. The Sierra Madre is in the distant background. April, 1947; elevation, about 1175 m.

FIG. 2. *Espinal* on a terrace above the flood plain of the Río Cuilco at Canibal is typical of this section of the Cuilco Valley in which the vegetation has been little disturbed by human activities. Note the sparse desert shrub on the valley slope in the background. April, 1947; elevation, about 1175 m.

PLATE III

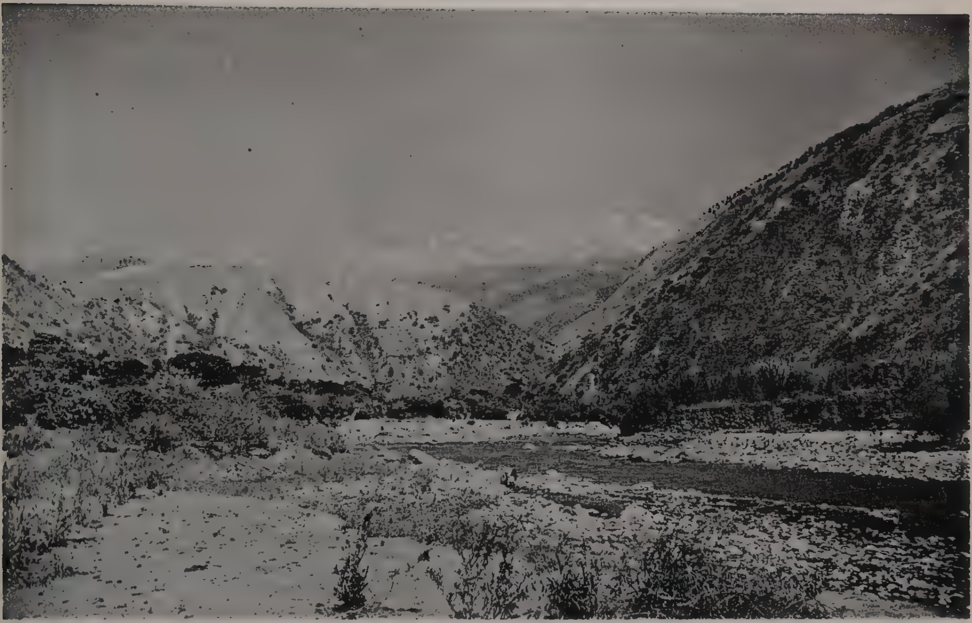

Fig. 1

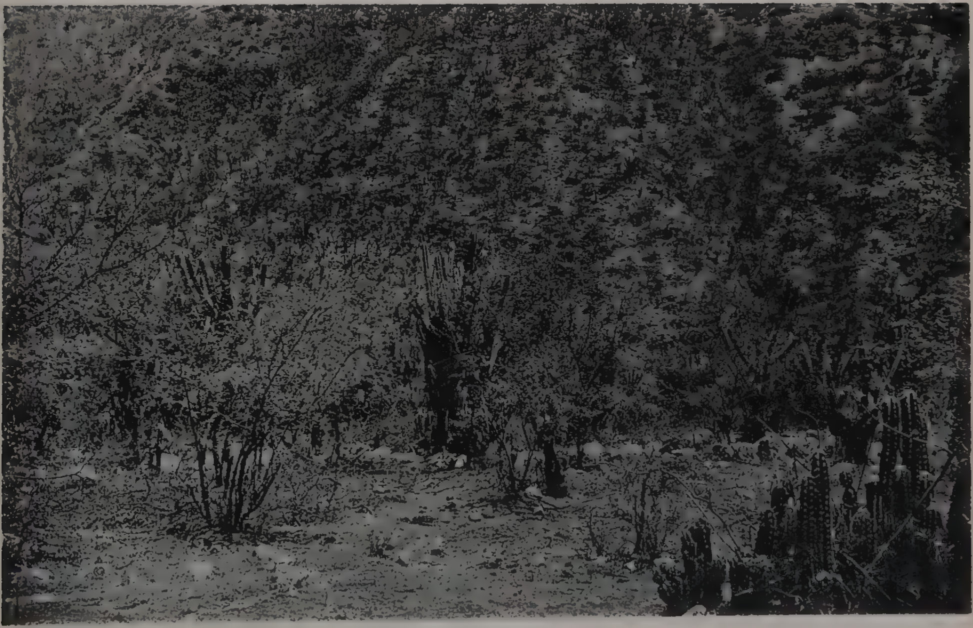

Fig. 2

PLATE IV

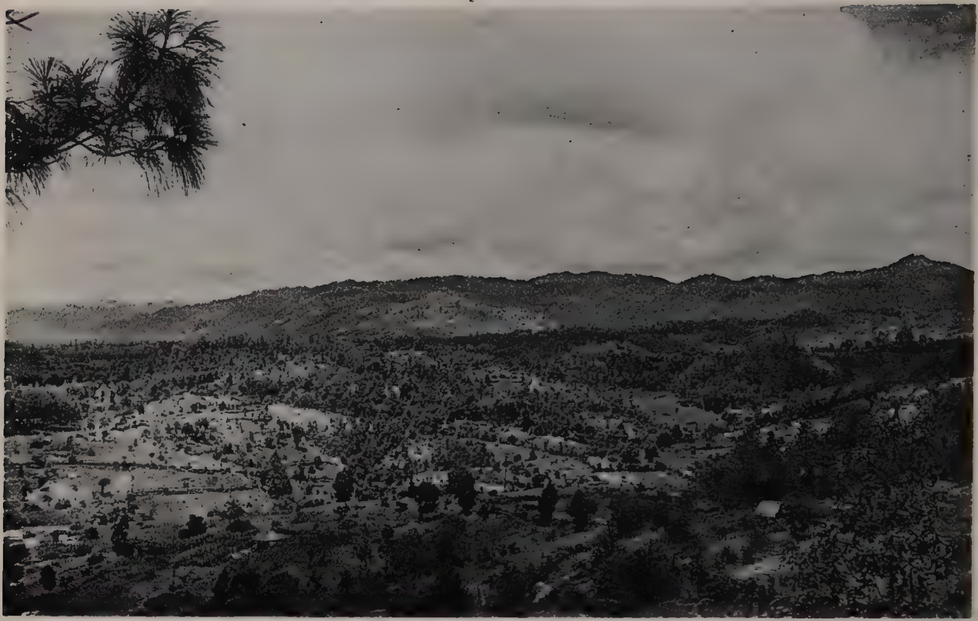

Fig. 1

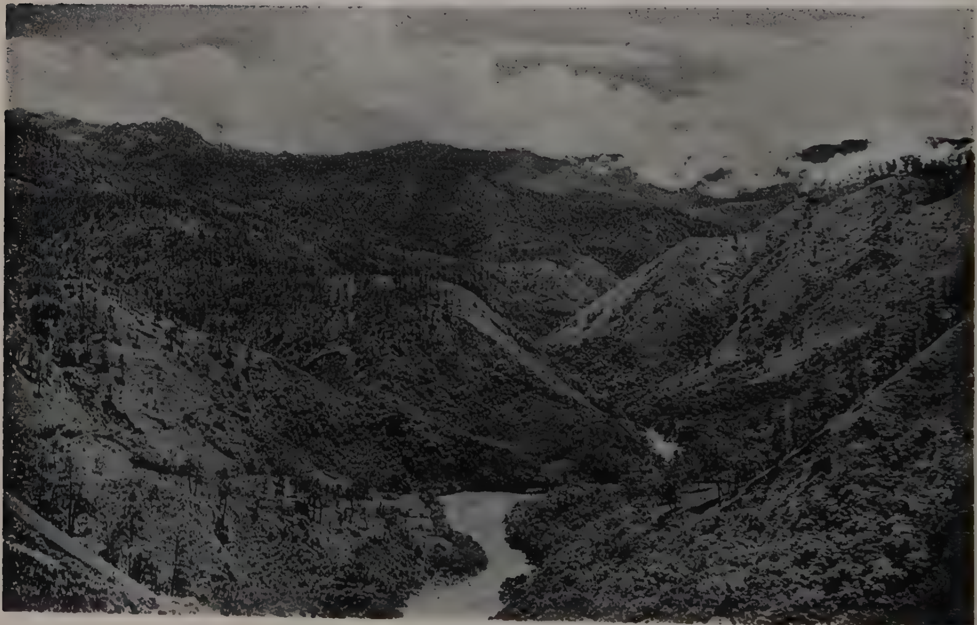

Fig. 2

PLATE IV

FIG. 1. The southwestern highlands of Guatemala on the divide between the watersheds of the Rios Negro and Motagua, looking eastward from the vicinity of Momostenango. Santa Cruz Quiché lies at the base of the ridge in the center background. These rolling uplands are typical of the oak-pine zone on the southwestern highlands and are encountered in the Huehuetenango region, which lies almost due north of the point from which this photograph was taken and which forms the highest break throughout the length of the subhumid corridor. The ridge in the background is the root of the Sierra de Chuacús at its junction with the Guatemalan Plateau. July, 1947; elevation, about 2200 m.

FIG. 2. Valley of the Río Negro at Chixoy below La Primavera, looking downstream with the Sierra de los Cuchumatanes in the background. The narrow valley bottom supports pine savanna, but in this vicinity are occasional thickets of stunted, broadleaf trees, and on the rocky slopes cacti and desert shrubs are not uncommon. Higher in the mountains an open oak and pine forest predominates. Even where clearing has not taken place, vegetation cover in this part of the valley is at best sparse. June, 1940; elevation of river, about 700 m.

PLATE V

FIG. 1. The Salamá Basin near the village of San Jerónimo, looking north. This is typical steppe which is rather heavily grazed. The somewhat denser stand of low trees seen as a thin dark line in the background marks a stream course. July, 1938; elevation, about 950 m.

FIG. 2. The oak-pine zone between the Salamá Basin and the Motagua Valley. The forests of these mountain slopes (north face of the Sierra de las Minas) are open except along the arroyos, where thickets of shrubs occur. Lumbering and grazing have altered somewhat the original cover. The pass between the Salamá Basin and the Motagua lies at about 1400 m. at this point. July, 1938; elevation, about 1200 m.

PLATE V

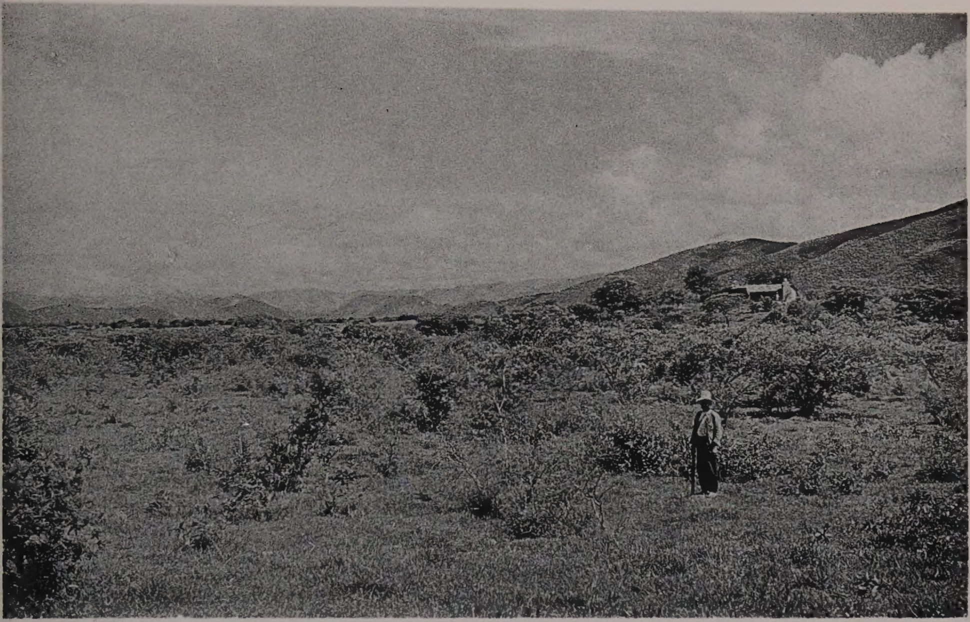

Fig. 1

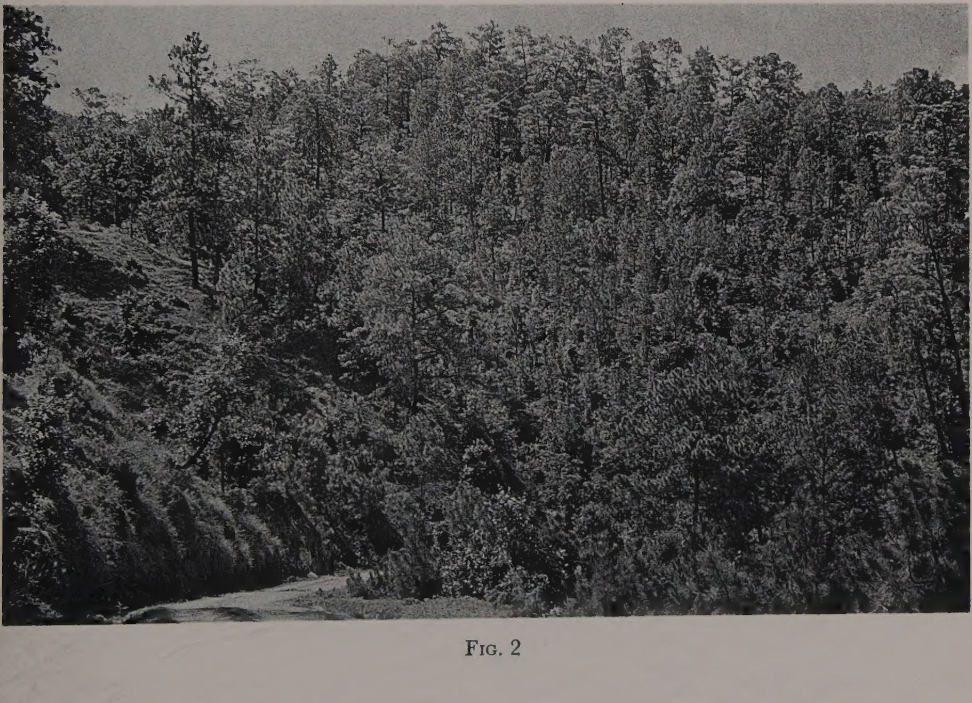

Fig. 2

PLATE VI

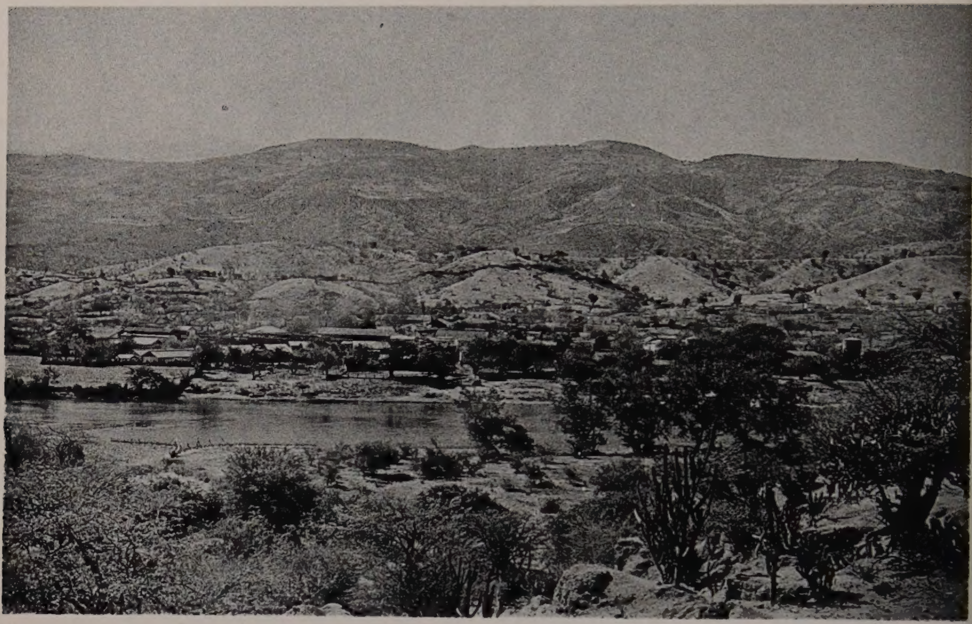

Fig. 1

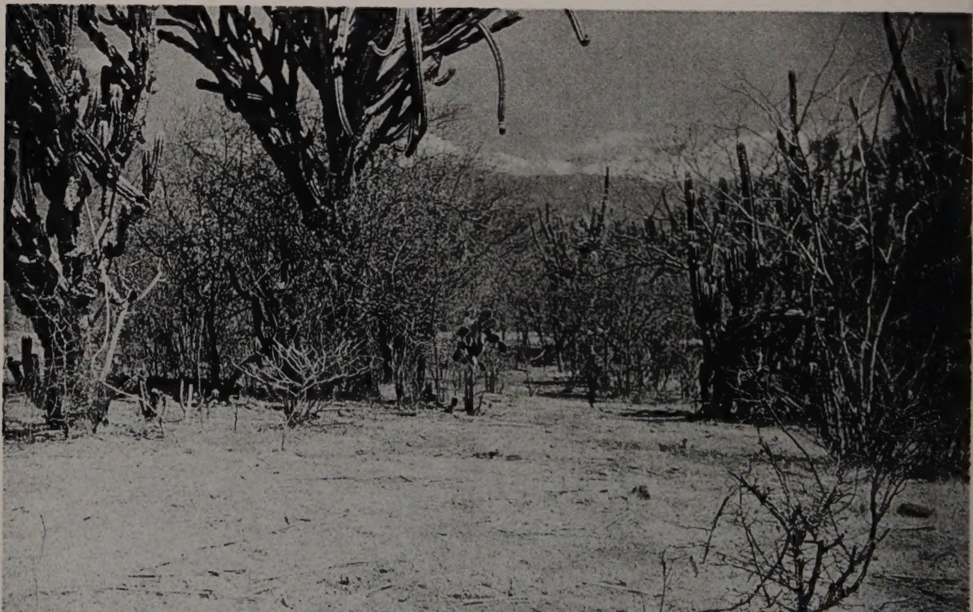

Fig. 2

PLATE VI

FIG. 1. The Motagua Valley at El Rancho, looking south. This is a typical desert landscape that prevails in this part of the valley. Two well-defined terraces are visible; one appears behind the village in the right background, and the village itself is situated on a lower one. Note particularly the sparse cover on the valley slopes in the background. February, 1952; elevation of El Rancho, 275 m.

FIG. 2. Cactus and mesquite flats in the vicinity of El Rancho. The giant cacti are the most conspicuous vegetation features of this part of the valley. Though in places the *espinal* is much denser than shown here, this is the more typical condition. The south face of the Sierra de las Minas is visible in the background. February, 1952; elevation, about 300 m.